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EXPERIMENTS ON THE SUPPOSED AUDITORY APPARATUS OF THE MOSQUITO.*

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OHM states in his proposition that the ear experiences a simple sound only when it receives a pendulum-vibration, and that it decomposes any other periodic motion of the air into a series of pendulum-vibrations, to each of which corresponds the sensation of a simple sound. Helmholtz, fully persuaded of the truth of this proposition, and seeing its intimate connection with the theorem of Fourier, reasoned that there must be a cause for it in the very dynamic constitution of the ear; and the previous discovery by the Marquis of Corti of several thousand† rods of graded sizes in the *ductus cochlearis* indicated to Helmholtz that these were suitable bodies to effect the decomposition of a composite sonorous wave by their co-vibrating with its simple harmonic elements. This supposed function of the Corti organ gave a rational expla-

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† "But all of the propositions on which we have based the theory of consonance and dissonance rests solely on a minute analysis of the sensations of the ear. This analysis could have been made by any cultivated ear, without the aid of theory, but the leading-thread of theory, and the employment of appropriate means of observation, have facilitated it in an extraordinary degree.

"Above all things I beg the reader to remark that the hypothesis on the co-vibration of the organs of Corti has no immediate relation with the explanation of consonance and dissonance, which rests solely on the facts of observation, on the beats of harmonics and of resultant sounds."—Helmholtz, Tonempfindungen, p. 342.

nation of the theorem of Ohm, and furnished "a leading thread" which conducted Helmholtz to the discoveries contained in his renowned work, "Die Lehre von den Tonempfindungen."* In this book he first gave the true explanation of timbre, and revealed the hidden cause of musical harmony, which, since the days of Pythagoras, had remained a mystery to musicians and a problem to philosophers.

It may, perhaps, never be possible to bring Helmholtz's hypothesis of the mode of audition in the higher vertebrates to the test of direct observation, from the apparent hopelessness of ever being able to experiment on the functions of the parts of the inner ear of mammalia. The cochlea, tunnelled in the hard temporal bone, is necessarily difficult to dissect, and even when a view is obtained of the organ of Corti, its parts are rarely *in situ;* and, moreover, they generally have had their natural structure altered by the acid with which the bone has been saturated to render it soft enough for dissection and for the cutting of sections for the microscope.

As we descend in the scale of development, from the higher vertebrates, we observe the parts of the outer and middle ear disappearing, while at the same time we see the inner ear gradually advancing toward the surface of the head. The external ear, the auditory canal, the tympanic membrane, and with the latter the now useless ossicles, have disappeared in the lower vertebrates, and there remains but a rudimentary labyrinth.

Although the homological connections existing between the vertebrates and articulates, even when advocated by naturalists, are certainly admitted to be imperfect, yet we can hardly suppose that the organs of hearing in the articulates will remain stationary or retrograde, but rather that the essential parts of their apparatus of audition, and especially that part which receives the aerial vibrations, will be more exposed than in higher organisms. Indeed, the very minuteness of the greater part of the articulates would indicate this, for a tympanic membrane placed in vibratory communication with a modified labyrinth, or even an auditory capsule with an outer flexible covering, would be useless to the greater number of insects for several reasons; first, such an apparatus, unless occupying a large proportion of the volume of an insect,

* According to Waldeyer, there are 6,500 inner and 4,500 outer pillars in the organ of Corti.

would not present surface enough for this kind of receptor of vibrations; and secondly, all non-aquatic vertebrates have an inner ear formed so as to bring the aerial vibrations, which strike the tympanic membrane, to bear with the greatest effect on the auditory nerve filaments, and the minuteness of insects precludes this condition. Finally, the hard test, characteristic of the articulates, sets aside the idea that they receive the aerial vibrations through the covering of their bodies, like fishes, whose bodies are generally not only larger and far more yielding, but are also immersed in water which transmits vibrations with $4\frac{1}{4}$ times the velocity of the same pulses in air and with a yet greater increase in intensity. For these reasons, I imagine that those articulates which are sensitive to sound, and also emit characteristic sounds, will prove to possess receptors of vibrations external to the general surface of their bodies, and that the proportions and situation of these organs will comport with the physical conditions necessary for them to receive and transmit vibrations to the interior ganglia.

Naturalists, in their surmises as to the positions and forms of the organ of hearing in insects, have rarely kept in view the important consideration of those physical relations which the organ must bear to the aerial vibrations producing sound, and which we have already pointed out. The mere descriptive anatomist of former years could be satisfied with his artistic faculty for the perception of form, but the student of these days can only make progress by constantly studying the close relations which necessarily exist between the minute structure of the organs of an animal and the forces which are acting in the animal, and which traverse the medium in which the animal lives. The want of appreciation of these relations, together with the fact that many naturalists are more desirous to describe many new forms than to ascertain the function of one well known form, which may exist in all animals of a class, has tended to keep many departments of natural history in the condition of mere descriptive science. Those who are not professed naturalists appreciate this perhaps more than the naturalists themselves, who are imbued with that enthusiasm which always comes with the earnest study of any one department of nature; for the perusal of those long and laboriously precise descriptions of forms of organs, without the slightest attempt, or even suggestion, as to

their uses, affects a physicist with feelings analogous to those experienced by one who peruses a well classified catalogue descriptive of physical instruments, while of the uses of these instruments he is utterly ignorant.

The following views, taken from the "Anatomy of the Invertebrata, by C. Th. v. Siebold," will show how various are the opinions of naturalists as to the location and form of the organs of hearing in the *Insecta.* "There is the same uncertainty concerning the organs of audition (as concerning the olfactory organs). Experience having long shown that most insects perceive sounds, this sense has been located sometimes in this and sometimes in that organ. But in their opinion, it often seems to have been forgotten, or unthought of, that there can be no auditory organ without a special auditory nerve, which connects directly with an acoustic apparatus capable of receiving, conducting and concentrating the sonorous undulations. (The author who has erred most widely in this respect is L. W. Clarke, in Mag. Nat. Hist., Sept., 1838, who has described at the base of the antennæ of *Carabus nemoralis* Illig. an auditive apparatus composed of an *Auricula*, a *Meatus auditorius externus* and *internus*, a *Tympanum* and *Labyrinthus*, of all of which there is not the least trace. The two white convex spots at the base of the antennæ of *Blatta orientalis*, and which Treviranus has described as auditory organs, are, as Burmeister has correctly stated, only rudimentary accessory eyes. Newport and Goureau think that the antennæ serve both as tactile and as auditory organs. But this view is inadmissible, as Erichson has already stated, except in the sense that the antennæ, like all solid bodies, may conduct sonorous vibrations of the air; but, even admitting this view, where is the auditory nerve? for it is not at all supposable that the antennal nerve can serve at the same time the function of two distinct senses.)

"Certain Orthoptera are the only Insecta with which there has been discovered, in these later times, a single organ having the conditions essential to an auditory apparatus. This organ consists, with the Acrididæ, of two fossæ or conchs, surrounded by a projecting horny ring, and at the base of which is attached a membrane resembling a tympanum. On the internal surface of this membrane are two horny processes, to which is attached an extremely delicate vesicle filled with a transparent fluid and representing a membranous labyrinth. This vesicle is in connection

with an auditory nerve which arises from the third thoracic ganglion, forms a ganglion on the tympanum, and terminates in the immediate neighborhood of the labyrinth by a collection of cuneiform, staff-like bodies with very finely-pointed extremities (primitive nerve-fibres ?), which are surrounded by loosely-aggregated, ganglionic globules. (This organ has been taken for a soniferous apparatus by Latreille. J. Müller was the first who fortunately conceived that with *Gryllus hieroglyphus* this was an auditory organ. He gave, however, the interpretation only as hypothetical; but I have placed it beyond all doubt by careful researches made on *Gomphoceros*, *Oedipoda*, *Podisma*, *Caloptenus* and *Truxalis*.")

"The Locustidæ and Achetidæ have a similar organ, situated in the fore-legs directly below the coxo-tibial articulation. With a part of the Locustidæ (*Meconema*, *Barbitistes*, *Phancroptera*, *Phylloptera*), there is on each side of this point a fossa, while with another portion of this family there are, at this same place, two more or less spacious cavities (auditory capsules) provided with orifices opening forward. These fossæ and these cavities have each, on their internal surface, a long-oval tympanum. The principal trachean trunk of the leg passes between two tympanums, and dilates, at this point, into a vesicle whose upper extremity is in connection with a ganglion of the auditory nerve. This last arises from the first thoracic ganglion, and accompanies the principal nerve of the leg. From this ganglion in question passes off a band of nervous substance, which stretches along the slightly excavated anterior side of the trachean vesicle. Upon this band is situated a row of transparent vesicles containing the same kind of cuneiform, staff-like bodies, mentioned as occurring with the Acrididæ. The two large trachean trunks of the fore-legs open by two wide, infundibuliform orifices on the posterior border of the prothorax, so that here, as with the Acrididæ, a part of this trachean apparatus may be compared to a *Tuba Eustachii*. With the Achetidæ, there is, on the external side of the tibia of the fore-legs, an orifice closed by a white, silvery membrane (tympanum), behind which is an auditory organ like that just described. (With *Acheta achatina* and *italica*, there is a tympanum of the same size, on the internal surface of the legs in question; but it is scarcely observable with *Acheta sylvestris*, *A. domestica* and *A. campestris*.)"

Other naturalists have placed the auditory apparatus of diurnal lepidoptera in their club-shaped antennæ; of bees at the root of their maxillæ; of *Melolontha* in their antennal plates; of *Locusta viridissima* in the membranes which unite the antenna with the head.

I think that Siebold assumes too much when he states that the existence of a tympanic membrane is the only test of the existence of an auditory apparatus. It is true that such a test would apply to the non-aquatic vertebrates, but their homologies do not extend to the articulates; and besides, any physicist can not only conceive of, but can actually construct other receptors of aerial vibrations, as I will soon show by conclusive experiments. Neither can I agree with him in supposing that the antennæ are only tactile organs, for very often their position and limited motion would exclude them from this function;* and, moreover, it has never been proved that the antennæ, which differ so much in their forms in different insects, are always tactile organs. They may be used as such in some insects; in others, they may be organs of audition; while in other insects they may, as Newport and Goureau surmise, have both functions; for, even granting that Müller's law of the specific energy of the senses extends to the insects, yet the anatomy of their nervous system is not sufficiently known to prevent the supposition that there may be two distinct sets of nerve fibres in the antennæ or in connection with their bases; so that the antennæ may serve both as tactile and as auditory organs; just as the hand, which receives at the same time the impression of the character of the surface of a body and of its temperature; or, like the tongue, which at the same time distinguishes the surface, the form, the temperature and the taste of a body. Finally, I take objection to this statement: "Newport and Goureau think that the antennæ serve both as tactile and auditory organs. But this view is inadmissible, as Erichson has already stated, except in the sense that the antennæ, like all solid bodies, may conduct sonorous vibrations of the air." Here, evidently, Siebold had not in his mind the physical relations which exist between two bodies which give exactly the same number of vibrations; for it is well known that when one of them vibrates, the other will be set into vibration by

*Indeed, they are often highly developed in themselves while accompanied by *palpi*, which are properly placed, adequately organized and endowed with a range of motion suitable to an organ intended for purposes of touch.

the impacts sent to it through the intervening air. Thus, if the fibrillæ on the antennæ of an insect should be tuned to the different notes of the sound emitted by the same insect, then when these sounds fell upon the antennal fibrils, the latter would enter into vibration with those notes of the sound to which they were severally tuned; and so it is evident that not only could a properly constructed antenna serve as a receptor of sound, but it would also have a function not possible in a membrane; that is, it would have the power of analyzing a composite sound by the co-vibration of its various fibrillæ to the elementary tones of the sound.

The fact that the existence of such an antenna is not only supposable but even highly probable, taken in connection with an observation I have often made in looking over entomological collections; viz: that fibrillæ on the antennæ of noctural insects are highly developed, while on the antennæ of diurnal insects they are either entirely absent or reduced to mere rudimentary filaments, caused me to entertain the hope that I should be able to confirm my surmises by actual experiments on the effects of sonorous vibrations on the antennal fibrillæ; also, the well known experiments of Hensen,* and the inferences of Dr. Johnston from anatomical studies of the antennæ of the Culex, encouraged me to seek in aerial insects for phenomena similar to those Hensen had found in the decapod, the Mysis, and thus to discover in nature an apparatus whose functions are the counterpart of those of the apparatus with which I gave the experimental confirmation of Fourier's theorem, and similar to the supposed functions of the rods of the organ of Corti.

The beautiful structure of the plumose antennæ of the male Culex is well known to all microscopists; and these organs at once recurred to me as suitable objects on which to begin my experiments. The antennæ of these insects are twelve-jointed and from each joint radiates a whorl of fibrils, and the latter gradually decrease in their lengths as we proceed from those of the second joint from the base of the antenna to those of the second joint from the tip. These fibrils are highly elastic and so slender that their lengths are over three hundred times their diameters. They taper slightly, so that their diameter at the base is to the diameter near the tip as 3 to 2.

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* Studies on the organ of hearing in the Decapods. "Journal of Scientific Zöology" of Siebold and Kölliker, Vol. xiii.

I cemented a live male mosquito with shellac to a glass slide and brought to bear on various fibrils a $\frac{1}{5}$th objective. I then sounded successively, near the stage of the microscope, a series of tuning-forks with the openings of their resonant boxes turned toward the fibrils. On my first trials with an Ut_4 fork, of 512 v. per sec., I was delighted with the results of the experiments, for I saw certain of the fibrils enter into vigorous vibration, while others remained comparatively at rest.

The table of experiments which I have given is characteristic of all of the many series which I have made. In the first column (A) I have given the notes of the forks in the French notation, which König stamps upon his forks. In the second (B) are the amplitudes of the vibrations of the end of the fibril in divisions of the micrometer scale; and in column (C) are the values of these divisions in fractions of a millimetre.

A.	B.	C.
Ut_2	·5 div.	·0042 mm.
Ut_3	2·5	·0200
Mi_3	1·75	·0147
Sol_3	2·0	·0168
Ut_4	6·0	·0504
Mi_4	1·5	·0126
Sol_4	1·5	·0126
B^{b}_4-	1·5	·0126
Ut_5	2·0	·0168

The superior effect of the vibrations of the Ut_4 fork on the fibril is marked, but thinking that the differences in the observed amplitudes of the vibrations might be owing to differences in the intensities of the various sounds, I repeated the experiment, but vibrated with lower intensities the forks which gave the greater amplitudes of co-vibration; and although I observed an approach toward equality of amplitude, yet the fibre gave the maximum swings when Ut_4 was sounded, and I was persuaded that this special fibril was tuned to unison with Ut_4 or to some other note within a semitone of it. The differences of amplitude given by Ut_4 and Sol_3 and Mi_4 are considerable, and the table also brings out the interesting observation that the lower (Ut_3) and the higher (Ut_5) harmonics of Ut_4 cause greater amplitudes of vibration than any intermediate notes. As long as a universal method for the determination of the relative intensities of sounds of different pitch remains undiscovered, so long will the science of acoustics remain

in its present vague qualitative condition.* Now, not having the means of equalizing the intensities of the vibrations issuing from the various resonant boxes, I adopted the plan of sounding, with a bow, each fork with the greatest intensity I could obtain. I think that it is to be regretted that König did not adhere to the form of fork, with *inclined prongs*, as formerly made by Marloye; for with such forks one can always reproduce the same initial intensity of vibration by separating the prongs by means of the same cylindrical rod which is drawn between them. Experiments similar to those already given revealed a fibril tuned to such perfect unison with Ut_3 that it vibrated through 18 divisions of the micrometer or ·15 mm., while its amplitude of vibration was only 3 div. when Ut_4 was sounded. Other fibrils responded to other notes, so that I infer from my experiments on about a dozen mosquitoes that their fibrils are tuned to sounds extending through the middle and next higher octave of the piano.

To subject to a severe test the supposition I now entertained, that the fibrils were tuned to various periods of vibration, I measured with great care the lengths and diameters of two fibrils, one of which vibrated strongly to Ut_3, the other as powerfully to Ut_4; and from these measures I constructed in homogeneous pine wood two gigantic models of the fibrils; the one corresponding to the Ut_3 fibril being about one metre long. After a little practice I succeeded in counting readily the number of vibrations they gave when they were clamped at one end and drawn from a horizontal position. On obtaining the ratio of these numbers I found that

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* I have recently made some experiments in this direction, which show the possibility of eventually being able to express the intensity of an aerial vibration directly in fraction of Joule's Dynamical Unit, by measuring the heat developed in a slip of sheet rubber stretched between the prongs of a fork and enclosed in a compound thermo-battery. The relative intensities of the aerial vibration produced by the fork when engaged in heating the rubber, and when the rubber is removed, can be measured by the method I described in the Amer. Jour. Sci., Feb., 1873. Of course if we can determine the amount of heat produced per second by a known fraction of the intensity, we have the amount produced by the vibration with its entire intensity. Then means can be devised by which the aerial vibration produced by this fork can always be reproduced with the same intensity. This intensity, expressed in fraction of Joule's unit, is stamped upon the apparatus, which ever afterward serves as a true measure for obtaining the intensities of the vibrations of all simple sounds having the same pitch as itself. The same operation can be performed on other forks of different pitch, and so a series of intensities of different periods of vibration is obtained expressed in a corresponding series of fractions of Joule's unit. Recent experiments have given one one hundred thousandth of a Joule's unit as the approximate dynamic equivalent of ten seconds of aerial vibrations produced by an Ut_3 fork, set in motion by intermittent electro-magnetic action and placed before a resonator.

it coincided with the ratio existing between the numbers of vibrations of the forks to which co-vibrated the fibrils of which these pine rods were models.

The consideration of the relations which these slender, tapering, and pointed fibrils must have to the aerial pulses acting on them, led me to discoveries in the physiology of audition which I imagine are entirely new. If a sonorous wave falls upon one of these fibrils so that its wave-front is at right angles to the fibril, and hence the direction of the pulses in the wave are in the direction of the fibril's length, the latter cannot be set in vibration; but if the vibrations in the wave are brought more and more to bear athwart the fibril it will vibrate with amplitudes increasing until it reaches its maximum swing of co-vibration, when the wave-front is parallel to its length and therefore the direction of the impulses on the wave are at right angles to the fibril. These curious surmises I have confirmed by many experiments made in the following manner. A fork which causes a strong co-vibration in a certain fibril is brought near the microscope, so that the axis of the resonant box is perpendicular to the fibril and its opening is toward the microscope. The fibril, in these circumstances, enters into vigorous vibration on sounding the fork; but, on moving the box around the stage of the microscope so that the axis of the box always points toward the fibril, the amplitudes of vibration of the fibril gradually diminish, and when the axis of the box coincides with the length of the fibril, and therefore the sonorous pulses act on the fibril in the direction of its length, the fibril is absolutely stationary and even remains so when the fork, in this position, is brought quite close to the microscope. These observations at once revealed to me a new function of these organs; for if, for the moment, we assume that the antennæ are really the organs which receive aerial vibrations and transmit them to an auditory capsule, or rudimentary labyrinth, then these insects must have the faculty of the perception of the direction sound more highly developed than in any other class of animals. The following experiments will show the force of this statement and at the same time illustrate the manner in which these insects determine the direction of a sonorous centre. I placed under the microscope a live mosquito, and kept my attention fixed upon a fibril which co-vibrated to the sound of a tuning-fork, which an assistant placed in unknown positions around the microscope. I then rotated the stage of the

instrument until the fibril ceased to vibrate, and then drew a line on a piece of paper, under the microscope, in the direction of the fibril. On extending this line, I found that it always cut within 5° of the position of the source of the sound. The antennæ of the male mosquito have a range of motion in a horizontal direction, so that the angle included between them can vary considerably inside and outside of 40°,* and I conceive that this is the manner in which these insects during night direct their flight toward the female. The song of the female vibrates the fibrillæ of one of the antennæ more forcibly than those of the other. The insect spreads the angle between his antennæ, and thus, as I have observed, brings the fibrillæ, situate within the angle formed by the antennæ, in a direction approximately parallel to the axis of the body. The mosquito now turns his body in the direction of that antenna whose fibrils are most affected, and thus gives greater intensity to the vibrations of the fibrils of the other antenna. When he has thus brought the vibrations of the antennæ to equality of intensity, he has placed his body in the direction of the radiation of the sound, and he directs his flight accordingly; and from my experiments it would appear that he can thus guide himself to within 5° of the direction of the female.

Some may assume from the fact of the co-vibration of these fibrils to sounds of different pitch, that the mosquito has the power of decomposing the sensation of a composite sound into its simple components, as is done by the higher vertebrates; but I do not hold this view, but believe that the range of co-vibration of the fibrils of the mosquito is to enable it to apprehend the varying pitch of the sounds of the female. In other words, the want of definite and fixed pitch to the female's song demands for the receiving apparatus of her sounds a corresponding range of co-vibration, so that instead of indicating a high order of auditory development it is really the lowest, except in its power of determining the direction of a sonorous centre, in which respect it surpasses by far our own ear.†

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* The shafts of the antennæ include an angle of about 40°. The basal fibrils of the antennæ form an angle of about 90,° and the terminal fibrils an angle of about 30°, with the axis of the insect.

† Some physiologists, attempting to explain the function of the semicircular canals, assume, because these canals are in three planes at right angles to each other, that they serve to fix in space a sonorous centre, just as the geometrician by his three coördinate planes determines the position of a point in space. But this assumption is fan-

The auditory apparatus we have just described does not in the least confirm Helmholtz's hypothesis of the functions of the organ of Corti; for the supposed power of that organ to decompose a sonorous sensation depends upon the existence of an auditory nerve differentiated as highly as the co-vibrating apparatus, and in the case of the mosquito there is no known anatomical basis for such an opinion. In other words, my researches show external co-vibrating organs whose functions replace those of the tympanic membrane and chain of ossicles in receiving and transmitting vibrations; while Helmholtz's discoveries point to the existence of internal co-vibrating organs which have no analogy to those of the mosquito, because the functions of the former are not to receive and transmit vibrations to the sensory apparatus of the ear, but to give the sensation of pitch and to decompose a composite sonorous sensation into its elements; and this they can only do by their connection with a nervous development whose parts are as numerous as those of the co-vibrating mechanism. Now as such a nervous organization does not exist in insects, it follows that neither anatomical nor functional relations exist between the co-vibrating fibrils on the antennæ and the co-vibrating rods in the organ of Corti, and therefore, that neither Hensen's experiments on the Mysis (assumed by Helmholtz to confirm his hypothesis), nor mine on the mosquito, can be adduced in support of Helmholtz's hypothesis of audition.*

The above described experiments were made with care, and I think that I am authorized to hold the opinion that I have established a physical connection existing between the sounds emitted by the female and the co-vibrations of the antennal fibrillæ of the male mosquito; but only a well established physiological relation

ciful and entirely devoid of reason; for the semicircular canals are always in the same dynamic relation to the tympanic membrane, which receives the vibration to be transmitted always in one way through the ossicles to the inner ear. Really, we determine the direction of a sound by the difference in the intensities of the effects produced in the two ears, and this determination is aided by the form of the outer ear and by the fact that man can turn his head around a vertical axis. Other mammalia, however, have the power of facilitating the determination of motion by moving the axis of their outer ears into different directions. It is also a fact that when one ear is slightly deaf, that the person unconsciously so affected always supposes a sound to come from the side on which is his good ear.

* Also, the organ of Corti having disappeared in the lower vertebrates, it is not likely that it would reappear in the articulata; and especially will this opinion have weight when we consider that the peculiar function of the organ of Corti is the appreciation of those composite sounds, whose signification mammals are constantly called upon to interpret.

between these co-vibrating parts of the animal and the development of its nervous system will authorize us to state that these are really the auditory organs of the insect. At this stage of the investigation I began a search through the zoological journals, and found nearly all that I could desire in a paper, in vol. iii, 1855, of the Quarterly Journal of the Microscopical Society, entitled "*Auditory apparatus of the Culex Mosquito*, by Christopher Johnston, M. D., Baltimore, U. S."

In this excellent paper I found clear statements showing that its talented author had surmised the existence of some of the physical facts which my experiments and observations have established.* To show that anatomical facts conform to the hypothesis that the antennal fibrils are the auditory organs of the mosquito, I cannot do better than quote the following from Dr. Johnston's paper:

"While bearing in mind the difference between *feeling a noise* and *perceiving a vibration*, we may safely assume with Carus—for a great number of insects, at least,—that whenever true auditory organs are developed in them, their seat is to be found in the neighborhood of the *antennæ*. That these parts themselves are, in some instances, concerned in collecting and transmitting sonorous vibrations, we hold as established by the observations we have made, particularly upon the *Culex mosquito;* while we believe, as Newport has asserted in general terms, that they serve also as tactile organs.

"The male mosquito differs considerably, as is well known, from the female; his body being smaller and of a darker color, and his head furnished with *antennæ* and *palpi* in a state of greater development. (Fig. 92.) Notwithstanding the fitness of his organs for predatory purposes, he is timid, seldom entering dwellings or annoying man, but restricts himself to damp and foul places, especially sinks and privies. The female, on the other hand, gives greater extension to her flight, and attacking our race, is the occasion of no inconsiderable disturbance and vexation during the summer and autumn months.

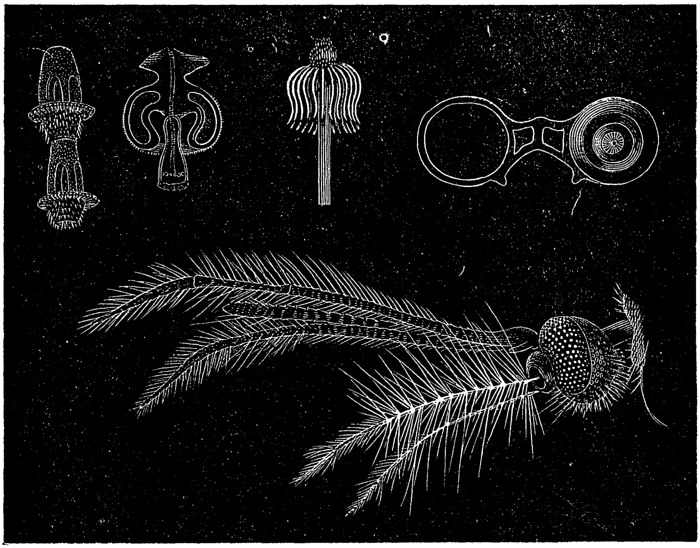
"The head of the male mosquito, about 0·67 mm. wide, is pro-

* A short time before the death of my friend, Prof. Agassiz, he wrote me these words: "I can hardly express my delight at reading your letter. I feel you have hit upon one of the most fertile mines for the elucidation of a problem which to this day is a puzzle to naturalists, the seat of the organ of hearing in Articulates."

vided with lunate eyes, between which in front superiorly are found two pyriform capsules nearly touching each other, and having implanted into them the very remarkable antennæ.

"The capsule, measuring about 0·21 mm., is composed of a horny substance, and is attached posteriorly by its pedicle, while anteriorly it rests upon a horny ring, united with its fellow by a transverse fenestrated band, and to which it is joined by a thin elastic membrane. Externally it has a rounded form, but internally it resembles a certain sort of lamp shade with a constriction near its middle;

Fig. 92.



Auditory Apparatus of the Mosquito.

and between this inner cup and outer globe there exists a space except at the bottom or proximal end, where both are united.

"The antennæ are of nearly equal length in the male and the female.

"In the male, the antennæ is about 1·75 mm. in length, and consists of fourteen joints, twelve short and nearly equal, and two long and equal terminal ones, the latter measuring (together) 0·70 mm. Each of the shorter joints has a fenestrated skeleton with an external investment, and terminates simply posteriorly,

but is encircled anteriorly with about forty *papillæ*, upon which are implanted long and stiff hairs, the proximal sets being about 0·79 mm. and the distal ones 0·70 mm. in length; and it is beset with minute bristles in front of each whorl.

"The two last joints have each a whorl of about twenty short hairs near the base.

"In the female the joints are nearly equal, number but thirteen, and have each a whorl of about a dozen small hairs around the base. Here, as well as in the male, the parts of the antennæ enjoy a limited motion upon each other, except the basal joint, which, being fixed, moves with the capsule upon which it is implanted.

"The space between the inner and outer walls of the capsule, which we term confidently the auditory capsule,* is filled with a fluid of moderate consistency, opalescent and containing minute spherical corpuscles, and which probably bears the same relation to the nerve as does the lymph in the scalæ of the cochlea of higher animals. The nerve itself, of the antenna, proceeds from the first or cerebral ganglion, advances toward the pedicle of the capsule in company with the large trachea, which sends its ramifications throughout the entire apparatus, and, penetrating the pedicle, its filaments divide into two portions. The central threads continue forward into the antenna, and are lost there; the peripheral ones, on the contrary, radiate outward in every direction, enter the capsular space, and are lodged there for more than half their length in *sulci* wrought in the inner wall or cup of the capsule.

"In the female the disposition of parts is observed to be nearly the same, excepting that the capsule is smaller, and that the last distal antennal joint is rudimental.

"The proboscis does not differ materially in the two sexes; but the palpi, although consisting in both instances of the same number of pieces, are very unlike. In the female they are extremely short, but in the male attain the length of 2·73 mm.; while the proboscis measures but 2·16 mm. They are curved upward at the extremity.

"* * * The position of the capsules strikes us as extremely favorable for the performance of the function which we assign to them; besides which there present themselves in the same light

*See fig 92.

the anatomical arrangement of the capsules, the disposition and lodgment of the nerves, the fitness of the expanded whorls for receiving, and of the jointed antennæ fixed by the immovable basal joint for transmitting, vibrations created by the sonorous undulations. The intra-capsular fluid is impressed by the shock, the expanded nerve appreciates the effect of the sound, by the quantity of the impression; of the pitch, or quality by the consonance of particular whorls of stiff hairs, according to their lengths; and of the direction in which the undulations travel, by the manner in which they strike upon the antennæ, or may be made to meet either antennæ in consequence of an opposite movement of that part.

"That the male should be endowed with superior acuteness of the sense of hearing appears from the fact, that he must seek the female for sexual union either in the dim twilight or in the dark night, when nothing but her sharp humming noise can serve him as a guide. The necessity for an equal perfection of hearing does not exist in the female; and, accordingly, we find that the organs of the one attain a development which the others never reach. In these views we believe ourselves to be borne out by direct experiment, in connection with which we may allude to the greater difficulty of catching the male mosquito.

"In the course of our observations we have arrived at the conclusion, that the antennæ serve to a considerable extent as organs of touch in the female; for the palpi are extremely short, while the antennæ are very movable, and nearly equal the proboscis in length. In the male, however, the length and perfect development of the palpi would lead us to look for the seat of the tactile sense elsewhere, and, in fact, we find the two apical antennal joints to be long, movable, and comparatively free from hairs; and the relative motion of the remaining joints very much more limited."

My experiments on the mosquito began late in the fall, and therefore I was not able to extend them to other insects. This spring I purpose to resume the research, and will experiment especially on those orthoptera and hemiptera which voluntarily emit distinct and characteristic sounds.